

A global catalog of primary reptile type specimens

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Abstract

We present information on primary type specimens for 13,282 species and subspecies of reptiles compiled in the Reptile Database, that is, holotypes, neotypes, lectotypes, and syntypes. These represent 99.4% of all 13,361 currently recognized taxa (11,050 species and 2311 subspecies). Type specimens of 653 taxa (4.9%) are either lost or not located, were never designated, or we did not find any information about them. 51 species are based on iconotypes. To map all types to physical

collections we have consolidated all synonymous and ambiguous collection acronyms into an unambiguous list of 364 collections holding these primary types. The 10 largest collections possess more than 50% of all (primary) reptile types, the 36 largest collections possess more than 10,000 types and the largest 73 collections possess over 90% of all types. Of the 364 collections, 107 hold type specimens of only 1 species or subspecies. Dozens of types are still in private collections. In order to increase their utility, we recommend that the description of type specimens be supplemented with data from high-resolution images and CT-scans, and clear links to tissue samples and DNA sequence data (when available). We request members of the herpetological community provide us with any missing type information to complete the list.

Key words: syntype, holotype, neotype, lectotype, herpetological collections, squamata, serpentes, sauria, testudines

Introduction

Over the past 260+ years at least 22,000 reptile species and subspecies have been described. Of these, 13,361 taxa are considered valid today (11,050 species and 2,311 subspecies, not counting nominate subspecies) (Uetz *et al.* 2019; Uetz & Stylianou 2018). Under the rules of the International Commission for Zoological Nomenclature, for a new species to be considered valid it must have at least one type specimen (ICZN Articles 71–75, see also Dubois 2017), even though other kinds of specific documentation such as illustrations (“iconotypes”), photographs or DNA-based information have been used and are extensively discussed in the literature (Chaladze 2017; Donegan 2008; Faundez 2017; Grandcolas 2017; Shatalkin & Galinskaya 2017; Zhang 2017). Nevertheless, physical type specimens remain a cornerstone and the gold standard of systematic biology, even as the type concept evolves with the addition of genome-sequence (Giribet 2016) or CT-microscan data (Broeckhoven *et al.* 2016).

Early species descriptions often did not clearly identify a primary type specimen, a problem that continues to produce taxonomic confusion to the present day. Later, especially at the end of the 19th century, several type specimens of equal status (“syntypes”) were commonly used. This latter practice is now rarely used, due to the confusion arising when a series of syntypes was a composite of multiple species (a surprisingly common occurrence e.g. Böhme 2005). Currently, best taxonomic practice requires that a single specimen be designated as a holotype (typically a voucher specimen, ideally with a tissue sample for DNA analysis), that is deposited in a public institution to guarantee easy scientific access. Ideally, additional specimens (paratypes) are nominated to represent ontogenetic, sexual, and intraspecific variation within a species, but paratypes are not considered here.

Even when holotypes were designated and are still extant, older descriptions were often brief and insufficient by today’s standards, especially when species are later added to the same genus. Consequently, the original types must be revisited and often require redescription.

While a type specimen provides a physical representation of the morphology of a species, an increasing number of new species are described primarily based on DNA sequences and molecular phylogenetic methods, with a physical description being provided but not necessarily allowing distinction in the field or even in a collection. An evolutionary species concept may delineate separate populations that are morphologically diagnosable, but it says little about whether those populations are reproductively isolated. It is not unusual for a single, morphologically defined species to harbor high levels of genetic variability corresponding to distinct intraspecific lineages (Harris *et al.* 2018; Hillis 2019). It is beyond the scope of this study to discuss the huge body of literature on species delimitation, but recent reviews discuss this problem in detail (e.g. Conix 2018; Fujita *et al.* 2012).

With increasingly fuzzy boundaries between populations and species, it becomes even more important to document biodiversity in as much detail as possible, not the least of which are the many ramifications related to conservation (Zachos 2013). Good collections of types (and additional specimens that capture the full variation within a species) are critical to assessing morphological and genetic diversity across its distributional range. Beyond sequencing a few hundred base pairs of mitochondrial DNA, the increased feasibility of sequencing complete genomes will allow us to analyze physical and physiological characters (Lippert *et al.* 2017), especially when supplemented with detailed morphological descriptions, habitat data, high-resolution photos, and CT scans (La Salle *et al.* 2016; Senna-Garaffoni & Lucci-Freitas 2017).

In order to make type collections of extant reptiles more accessible, and to get a better understanding of their physical location, we have tracked down the primary types of almost all currently accepted reptile species and subspecies. Other types (such as paratypes and/or paralectotypes) have been added, when available, but no attempt was made to complete their lists. This compilation facilitates taxonomic research by helping to integrate collection data

with those from other sources, such as georeferenced data (Erp *et al.* 2014), photos as derived from citizen science projects (such as iNaturalist.org), and many others.

Another important goal of our project is to standardize collection acronyms, a problem that has inhibited comparisons between collections and datasets for many years. For some collections, more than half a dozen acronyms have been used across multiple publications, which makes it extremely difficult to keep track of their specimens. This becomes an even bigger problem when specimens are cross-referenced, for example in DNA sequence databases. For example, publications have referred to the *Raffles Museum of Biodiversity Research* of the *National Museum of Singapore* as either LKCNHM, NMS, NUS, RM, RMBR, ZRCS, or USDZ as the collection acronym. We have consolidated such acronyms into a single acronym (here: ZRC, for *Zoological Reference Collection* for the *Raffles Museum* following Sabaj (2016) and replaced ambiguous acronyms with unique ones whenever necessary (see Methods).

Materials and methods

Primary type information was collected from numerous sources including published type catalogs, books, taxonomic monographs, species descriptions, unpublished museum collection catalogues and databases such as online type catalogs (see references and **Supplementary Table S1**). Not all literature sources can be cited here, or in the table, given that the type information for thousands of species was extracted from their original descriptions, taxonomic revisions, or from collection catalogues. These references can be found in the Reptile Database and in Uetz & Stylianou (2018). Note that we focus on primary types: holo-, lecto-, neo- and syntypes. Secondary type specimens (e.g., allotypes, paratypes) were beyond the feasible scope of this compilation. However, the Reptile Database lists paratypes for more than 2000 species. While we could have opted to delete paratypes to make this compilation more consistent, we decided to include as much information as was available to us. The type catalog in the Reptile Database is an ongoing project, so we will try to include all secondary types in the future. For a more detailed definition of primary type specimens see ICZN (1999: Chapter 13, Article 61, and chapter 16, Articles 71–75). Importantly, we only consider types of currently accepted species and subspecies. The primary types of some junior synonyms can be found in the species accounts within the Reptile Database, although this list is not complete. Taxon names, type information, and literature data, were stored internally in a Filemaker database and processed using custom scripts written in Filemaker Pro 16, Python 3, and R 3.5.

Collection acronyms. Museum acronyms were initially obtained from the aforementioned sources and then standardized using Sabaj's symbolic code table (Sabaj 2016). Note that we use the more common term “*acronym*” although they are technically *abbreviations*. Synonymous collection acronyms, such as NMP = *National Museum Prague* and *Natal Museum Pietermaritzburg* were re-assigned so that no ambiguity remains (here: NMP for Prague and NMSA for Pietermaritzburg). In several cases, we reverted to previously used acronyms instead of creating completely new ones to ensure that each acronym is unique (e.g. NMBA for the Basel Museum even though Sabaj uses NMB). Sabaj's table still contains about 170 ambiguous acronyms, which we disambiguated *only* for collections that hold reptile types but *not* for other collections (i.e., those without reptile types or those that keep amphibians or fish only). If types were transferred from one collection to another, the current collection acronym and catalog number is used. However, older collections (and catalog numbers) are given when available. Ambiguous acronyms in Sabaj (2016) that we re-assigned are indicated in a list of collections and their acronyms (**Supplementary Table S2**).

Results and discussion

We assembled data for primary type specimens (or at least the collections that house them) for 13,282 of the 13,361 (99.4%) currently recognized reptile species and subspecies listed in the Reptile Database. That is, for 13,282 reptile taxa we found *some* information about their primary types, including those considered lost or unknown, but only 12,658 taxa appear to have known *existing* types. These numbers only include currently accepted names but omit synonyms. A common problem was to associate specimens with collections and institutions. Many species descriptions do not give explicit collection information or do so only indirectly, especially in the older literature. For instance, if an author is affiliated with a certain museum, it is often tacitly assumed that all described specimens are

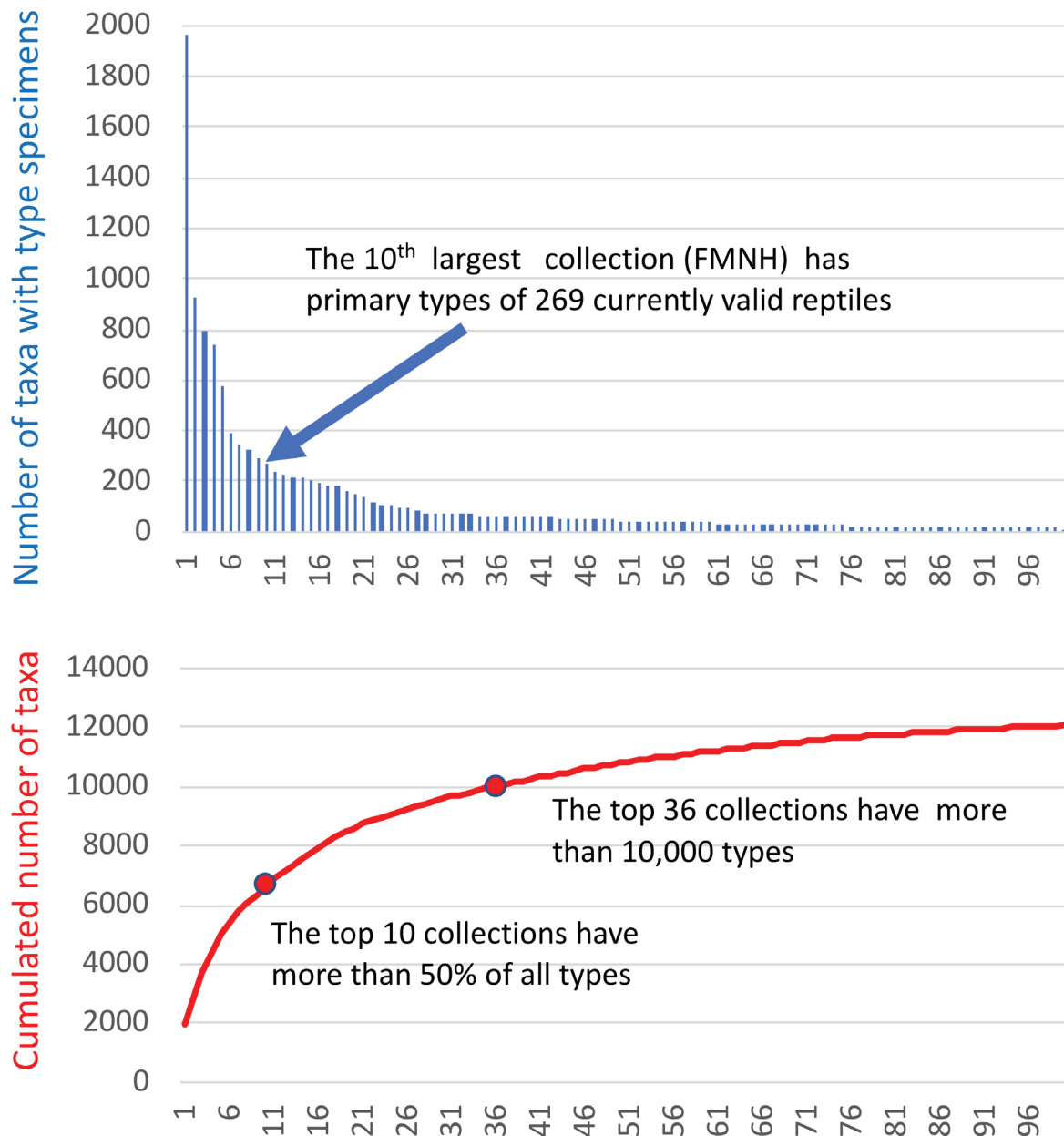
maintained in that collection. This is *usually* true, but exceptions are common. For instance, the types of at least 80 species described by George Albert Boulenger are not kept in the Natural History Museum, UK (NHMUK, formerly British Museum, Natural History, BMNH) where he spent most of his working life (see **Supplementary Table S3**). Boulenger, like many other taxonomists, visited many other collections and other herpetologists sent him specimens only as loans so that his authorship may obscure the whereabouts of his types.

Type collections. The primary types of currently recognized reptile species and subspecies are kept in 364 collections around the world (**Table 1, Supplementary Table S2, Figure 3**). Only 24 collections maintain primary types of more than 100 species and subspecies, another 88 possess 10 to 98 types, but the vast majority (~250 collections) have fewer than 10. In fact, 107 collections have only one primary type (**Fig. 1**). We did not attempt to catalog all other types, such as paratypes, because they are often spread across multiple institutions and are mentioned inconsistently in revisionary works. Occasionally there are also national idiosyncrasies. For instance, in France the primary types of new species are typically deposited in the National Museum (MNHN, Paris) while one or more paratypes are often kept in smaller, local collections.

TABLE 1. The 25 largest reptile type collections, as measured by total number of species and subspecies (“taxa”) with primary types. The total number of reptile specimens per collection is given as a reference, if available. Included are all collections that have the types of more than 92 species. Only currently accepted (“valid”) taxa are considered, i.e. types of synonyms are excluded. For a published catalog of type catalogs see Crumly (1990). Collection acronyms and other details are spelled out in **Supplementary Table S2**, which also contains a list of the remaining 348 collections that hold primary types. A list of published type catalogs for these and other collections are provided in **Supplementary Table S1**. For the list of primary type specimens see **Supplementary Table S3**.

Acronym	Location	Specimens ¹	Taxa
1. BMNH ²	London, UK	150,000	1968
2. MNHN	Paris, France	83,000	929
3. MCZ	Cambridge, USA	191,000*	797
4. USNM	Washington DC, USA	195,092	740
5. ZMB	Berlin, Germany	~60,000	575
6. SMF	Frankfurt, Germany	75,000	394
7. WAM	Perth, Australia	138,760	352
8. AMNH	New York, USA	172,681	323
9. CAS	San Francisco, USA	185,153	291
10. FMNH	Chicago, USA	122,583	269
11. RMNH+ZMA ³	Leiden, Netherlands	?	241
12. ANSP	Philadelphia, USA	19,000	222
13. NMW	Vienna, Austria	95,000	213
14. UMMZ	Ann Arbor, USA	140,630	212
15. ZFMK	Bonn, Germany	65,693	202
16. QM	Brisbane, Australia	54,759	192
17. ZISP	St. Petersburg, Russia	~300,000*	180
18. ZSM	Munich, Germany	110,000	179
19. ZSI	Kolkata, India	?	164
20. AMS	Sydney, Australia	125,992	153
21. MZUSP	São Paulo, Brazil	120,000*	136
22. DNMNH	Pretoria, South Africa	?	122
23. MSNG	Genova, Italy	?	106
24. NRM	Stockholm, Sweden	8,000*	104
25. KU	Lawrence, KS, USA	162,780	98

¹Numbers with asterisks (*) from collection websites, April 2019. ²Now also as NHMUK. ³RMNH and ZMA used to be separate collections with their own catalogue numbers but are now merged with ZMA specimens retaining their original catalog numbers.



Collections (ordered by number of taxa with primary types)

FIGURE 1. Number of taxa with primary type specimens in the 100 largest collections (above) and the cumulated number of (sub-) species with primary types in these collections (below). The collections are sorted by number of currently valid taxa with primary type specimens (numbers do not represent number of specimens). These 100 collections maintain ~90% of all type specimens. The remaining 264 collections maintain the remaining ~10% of types.

There is no strong correlation between the total number of specimens and the number of type specimens (**Table 1**). Large collections can have relatively few types and vice versa. For instance, The Steinhardt Museum of Natural History in Tel Aviv (TAU) has about the same number of reptile specimens as the Academy of Natural Sciences of Philadelphia (ANSP), namely about 19,000, but TAU has only primary types of two species while ANSP has 224. The growth of collections depended not only on their access to type material, but more generally on expeditions to and shipments from what were colonial territories. It is also notable that the growth of many collections was driven by a few individuals (**Fig. 2**).

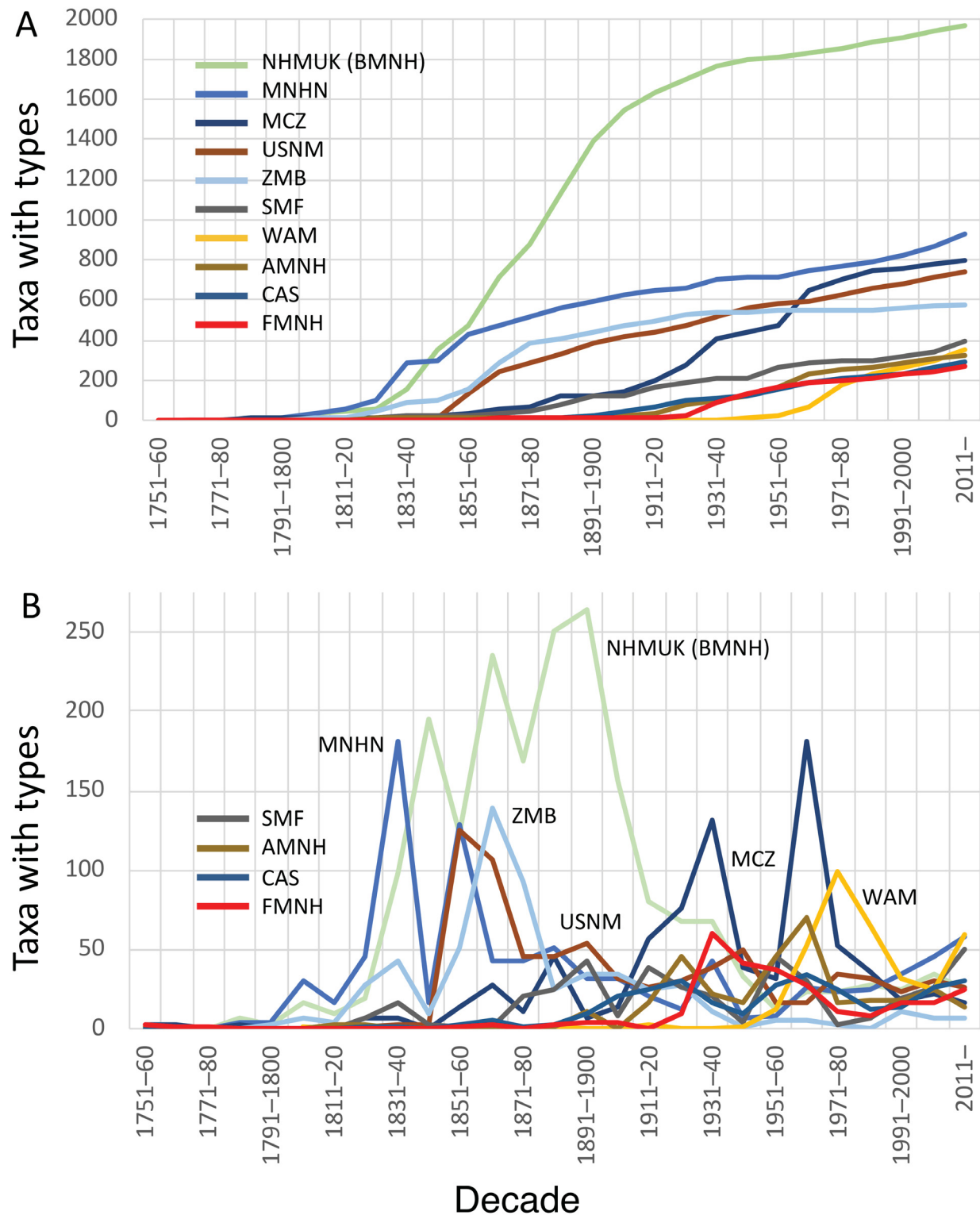


FIGURE 2. Growth of primary type material in the top 10 collections. (A) Collections are sorted by decade and number of currently valid species and subspecies with primary type material held in the collection (numbers do not represent number of specimens or total collection size). **(B)** Growth of type material given as number of new taxa.

Political rules and laws do affect where types are deposited. Many countries did not have institutions able to accept and/or care for collections in previous centuries. As a result, specimens were often taken back to the countries from which the expeditions originated and incorporated into their institutions (e.g., British Museum of Natural His-

tory). After being exploited during colonial times, several countries now require that types specimens be deposited in the country where the specimens were collected (e.g. India, Brazil, Indonesia, and others).

In order to get a better sense of where collections and their types are geographically located, we geo-referenced them (**Fig. 3**). Of the 364 collections identified by us, 83 are in Europe (including western Russia), 87 are in Asia (including five in Western Asian countries such as Georgia), 83 are in South America, 42 are in North America, 24 are in Central America or Cuba, 17 are in Africa or Madagascar, 15 are in the Middle East (including Turkey), and 13 are in Australia, New Zealand, or Oceania (Fiji).

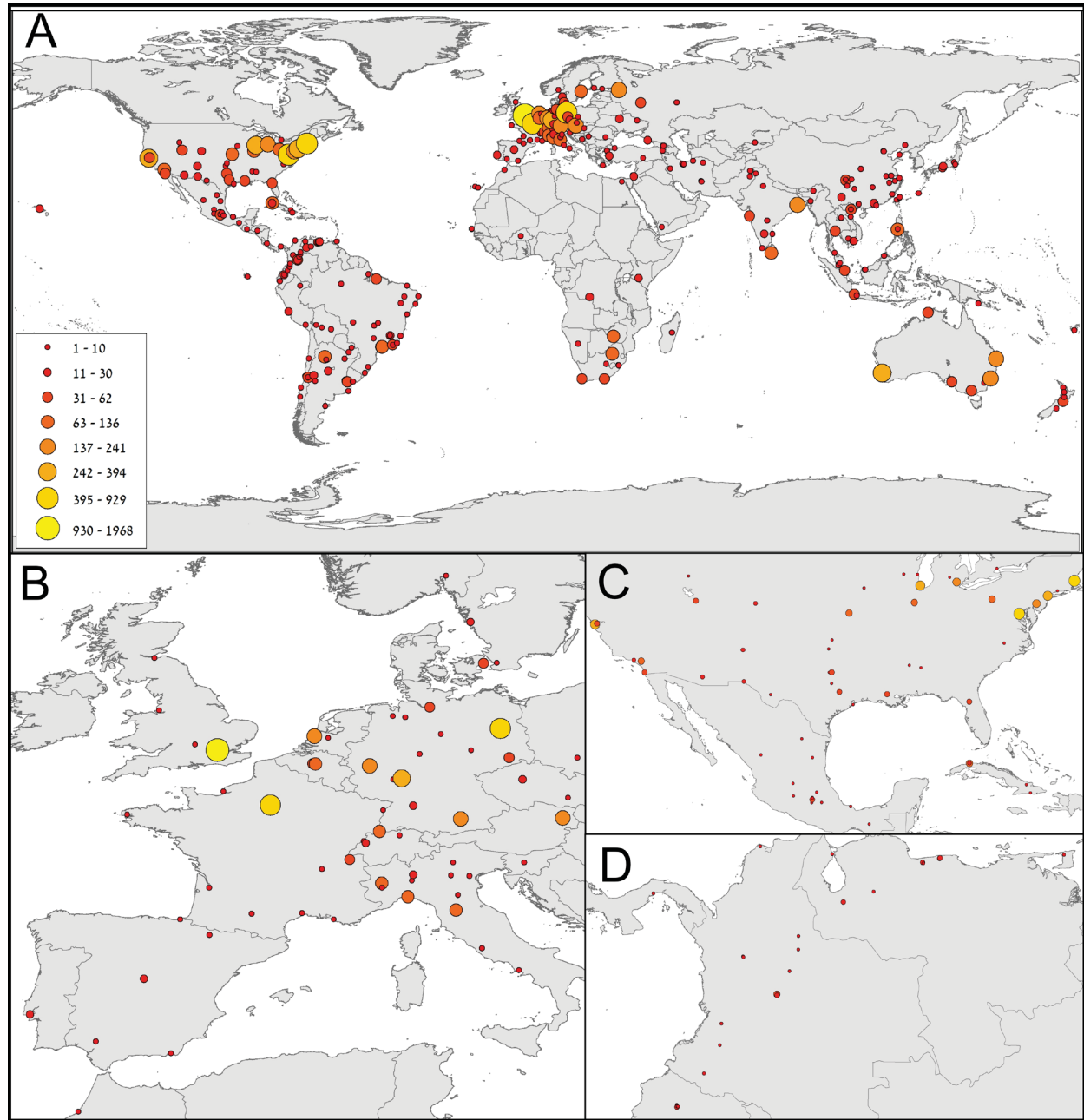


FIGURE 3. Location of all 364 collections that hold primary reptile type specimens. (A) Global overview with number of taxa with primary types indicated as colored discs. Areas with large numbers of collections are enlarged in (B) Europe, (C) North America, and (D) Northern South America. Size scale from A does not apply to B–D. Use colors instead.

Private collections. Some taxonomists have not deposited their types in public collections but instead retained them in their own, private collection. The original species descriptions often contained “private” collection acronyms, e.g., “EHT-HMS” for the specimens collected by Edward H. Taylor and Hobart M. Smith. Most of their types were later donated to public collections such as the Field Museum of Natural History in Chicago (FMNH) or to the

University of Illinois Museum (UIMNH; now curated by the Illinois Natural History Survey, INHS). This practice has confused herpetologists for decades and is still not entirely abolished, even though most scientific journals will only publish new species descriptions when the primary type is deposited in a public collection. Based on original publications and subsequent updates, our compilation identified the types of 28 species that are probably still kept in private collections (listed in **Supplementary Table S3**), something we hope will soon change.

Several types were reported as **live specimens** and their current whereabouts are not always clear. For instance, the holotype of *Gallotia intermedia* Barrbadillo *et al.* 1999 was still alive in 2017 (Jaime A. de Urioste, pers. comm., 17 June 2017), about 18 years after its original description. Another example is the type of *Conolophus marthae* Gentile & Snell 2009, which was captured and photographed, tagged with a Passive Integrated Transponder (PIT) and apparently released again (Frick 2010). While this approach has been criticized (Dubois 2009), at least tissue was collected and is now preserved at the MCZR (Civic Museum of Zoology, Rome, not to be confused with the Reptile collection at the Museum of Comparative Zoology in Cambridge, MA, abbreviated as MCZ-R). In this particular case, photos have been also deposited at Morphobank (<http://www.morphobank.org>), but see discussion and references about photos above.

Some private collections are difficult to distinguish from public institutions, especially if they use their own acronyms. The aforementioned collection of Edward H. Taylor and Hobart M. Smith (“EHT-HMS”) is among the most cited ones, but there are several that are less well-known, e.g. “CARE”, the “*colección de A. R. Estrada*”. Some private collections have also promoted themselves as “museums”, such as Farhang Torki’s private collection in Iran, which has been cited as *Farhang Torki Herpetological Museum* (FTHM), or as *Farhang Torki Ecology und Herpetology Center for Research* (FTEHCR). Some FTHM/FTEHCR types were recently transferred to the Museum Koenig in Bonn, Germany (ZFMK), and the Paris museum (MNHN-RA).

Missing, lost, and unknown types. The loss or “mis-placement” of types has been a common problem for centuries (e.g. Taylor 1944). To this end, we tried to track down many types that were reported as lost. Despite our efforts, we were not able to locate the type specimens for 653 species or subspecies (~4.9% of all taxa). For 79 species or subspecies, we did not find any information about types in the literature. For the remaining 574, the types have either been reported as lost (293), unknown / not located (236), were simply never designated or not specified in their original descriptions (45). We distinguish these cases in **Supplementary Table S3**, but they can be broken down into two simple groups: no types designated or no information available to us ($79 + 45 = 124$ taxa) or information in the literature explicitly suggests the types cannot be located or have been lost ($236 + 293 = 529$ taxa). The 51 taxa with iconotypes are included in the 653 taxa without specimens although in some cases physical specimens may exist.

We have plotted the aforementioned 653 lost or unknown types against the number of species described during the past 260 years (**Fig. 4**). Not surprisingly, the types of species described in the late 1700s and early 1800s have been lost most often. While many Linnaean types still exist, roughly half of all 261 species described in the 1700s have lost their original types (not counting more than 30 whose lost types have been replaced by neotypes).

Many types were lost during World War II (e.g., in Hamburg, Dresden, München, and Stuttgart, Germany, and Manila in the Philippines) or during catastrophic fires (e.g. Lisbon in 1978 or the Instituto Butantan, São Paulo in 2010). Many of those cases may require the designation of a lectotype (if syntypes are available) or neotypes although the latter are only justified when taxonomic issues can only be resolved with a type.

Many type catalogs were published a long time ago, and may no longer accurately represent the current state of their type specimens. It routinely happens that “lost” types resurface. In fact, several types that had been considered lost for decades have been re-discovered. For instance, Wagner *et al.* (2009) considered the type of *Agama agama* Linnaeus 1758 as being lost and thus designated a neotype (ZFMK 15222). However, Linnaeus’s holotype does still exist in Uppsala (UUZM 32), meaning that the neotype loses its status as a type specimen. Notably, Mediannikov *et al.* (2012) then used ZFMK 15222 as the holotype for a new species, *Agama wagneri* Trape *et al.* 2012, which was then synonymized with *A. agama* by Leache *et al.* (2014), demonstrating the sometimes convoluted paths of types and names.

Types of genera (type species). A type species plays a special role in taxonomy as it is permanently tied to and thereby helps define a particular genus. We were not able to find any type specimen information for the type species of 144 of the currently valid 1198 reptile genera. These types are either unknown, lost, were never formally designated or simply “not located” (see above). This mostly affects genera described in the 19th century, e.g. the type species of the genera *Proctoporus* Tschudi 1845 and *Psammophilus* Fitzinger 1843, which do not seem to have extant

type specimens (David *et al.* 2011; Dubois 2010). Type species without known types are listed in **Supplementary Table S3**.

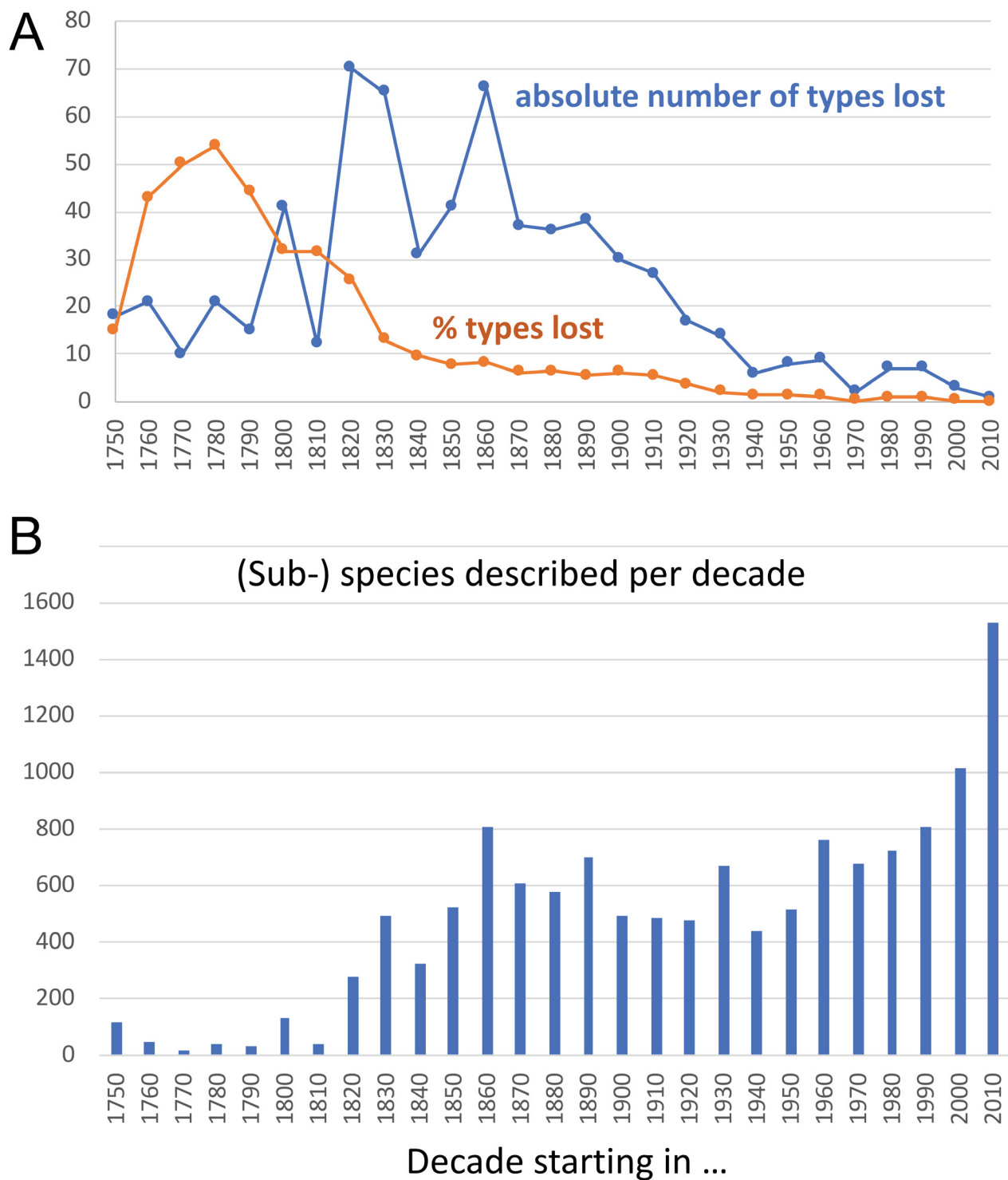


FIGURE 4. The loss of types over 260 years of reptile taxonomy. (A) Most of the 653 lost or not located types belong to species described in the late 1700s and early 1800s. While many Linnaean types still exist, roughly half of all original types from the 1700s are now lost. **(B)** While the number of described species and subspecies steadily increased, the loss of types decreased (A). See **Supplementary Table S3** for individual types.

Interestingly, 23 type species have been designated based on **iconotypes**, i.e. published illustrations, often in historical papers such as *Locupletissimi Rerum naturalium Thesauri accurata Descriptio...* (Seba 1734). In most cases, the physical type specimens appear to be lost, but may have never existed in a collection, for instance, when the animal was drawn from a live specimen. *Lyriocephalus scutatus* (Linnaeus 1758), for example, is the type species of the genus *Lyriocephalus* Merrem 1820. Its iconotype is based on Seba (1734, pl. 109. fig. 3), but no physical type is known to exist.

Because of the obvious limitations of basing a species description on illustrations, it may be necessary to designate neotypes for many of these species. Freshly collected specimens from the type localities (topotypes) can also yield DNA samples for genomic sequencing and thus may solve multiple problems at once.

Digitization of type collections. Several projects around the world have started to digitize and unite museum collection data into more comprehensive digital catalogues of specimens (not just types). In the US, the National Science Foundation (NSF) has supported efforts such as VertNet (Guralnick *et al.* 2016) and iDigBio (<https://www.idigbio.org>) for many years. Internationally, GBIF (<https://www.gbif.org>) has worked on similar projects with a focus on geo-referencing specimen localities (Constable *et al.* 2010). However, we do not know what fraction of vertebrate collections and their types have so far been included within these larger scale projects.

Those efforts should not be confused with other projects that digitize the actual specimens, e.g. by photographing or CT-scanning (Broeckhoven *et al.* 2016). The latter projects lag far behind the digitization of collection ledgers and catalogues, and thus will take many more years to complete.

DNA and tissue collections of types. With the advent of DNA sequencing, it has become increasingly important to collect tissue or DNA samples in addition to the actual type specimen, in part because formalin fixation (commonly used for reptile vouchers) often damages DNA and makes its extraction extremely difficult. This makes collection management challenging, as tissue and DNA samples must be stored separately from their type specimens. Digital links between specimen vouchers, tissues and DNA extracts are critical. We strongly recommend that the metadata for tissues and DNA extracts include the same standard collection acronym and catalog number (and specimen number if appropriate) to direct users of sequence data to the precise specimen voucher. Often it is not indicated in published type information whether tissue samples are available and where they are stored. In theory, it should be easy to distribute available DNA extracts from type specimens to multiple collections, but this is rarely done. For numerous applications, genomic DNA would be a much better resource, especially since mtDNA is of limited use beyond bar-coding and phylogenetic studies. For instance, genomic DNA allows us to investigate the genetic basis of many biological traits such as venom (Junqueira-de-Azevedo *et al.* 2016), coloration (Saenko *et al.* 2015), ecological adaptations (Li *et al.* 2018) or morphology such as limb loss (Thompson *et al.* 2018).

The National Center for Biotechnology Information (NCBI), which maintains both GenBank and the NCBI taxonomy database (Federhen 2012), has recently started to include specimen information, including type data, into their database (Federhen 2015). This allows researchers to refer a specific DNA sequence to a voucher specimen, if the latter exists. Given that specimens in collections may be misidentified and species names may change due to taxonomic revision, this is a welcome improvement that will help map sequences to specimens. For example, accession MF154856 in GenBank contains the RAG1 sequence from the holotype of the gecko *Goggia matzikamaensis* (Heinicke *et al.* 2017), with specimen voucher and the type material qualifiers: *specimen_voucher*="MCZ:R-192186" and *type_material*="holotype of *Goggia matzikamaensis*".

Outlook. While type specimens remain critical to taxonomy, an ever-improving digital infrastructure makes it increasingly easy to gain virtual access to type specimens. Access is facilitated both by databases such as the Reptile Database, but also by access to DNA databases and 3D scans of specimens. In the near future, researchers will be able to remotely investigate a specimen using computerized 3D visualizations of external (e.g. <http://digitallife3d.org>) as well as internal (<https://www.morphosource.org>) anatomy. We are still a long way from predicting phenotypes from genome sequences, and thus type specimens will continue to be required for a long time as the standard for taxonomic reference. We therefore expect this catalog will facilitate future research on the taxonomy and systematics of reptiles by increasing the visibility and utility of the primary types and the collections that house them.

Availability and updates to this catalog. The type catalogue described in this paper is available as a downloadable spreadsheet in **Supplementary Table S3**. The data will be continuously updated in the Reptile Database (<http://www.reptile-database.org>) but we also depend on feedback from curators and taxonomists. We will continuously update cross-references to other databases such as the NCBI taxonomy; accordingly, curators are encouraged to submit updates to this resource as well.

Readers are requested to send corrections and additions to the corresponding author or the curator of one the collections indicated in the author list.

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Supplementary Tables (Excel spreadsheets):

TABLE S1: Bibliography of published type catalogs, with collection acronyms matching Table S2.

TABLE S2. All collections with primary reptile types, with acronym, number of species and subspecies with primary types, location (country, city, and global region). If acronym is ambiguous in Sabaj (2016) all ambiguous acronyms have been dis-ambiguated in this list.

TABLE S3. All 13,282 reptile species and subspecies from the Reptile Database, with authors, year of description, subspecies flag, type kind (e.g. holotype or neotype), collection acronym, and type details (from the Reptile Database) (**Sheet 1**). Note that the types_info field (column E) corresponds to the free text in the Reptile Database. **Sheet 2** lists all taxa *without* known types (note: this table is redundant with Sheet 1), including type species of genera without types. **Sheet 3** provides a summary of taxa without known types (counting unknown, lost, etc. types). **Sheet 2** lists *type species* without known type specimens.